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Mycorrhizae in Sedges as Related to Root Character and Its Ecological Significance

T.MUTHUKUMAR, K.UDAIYAN, K.VASANTHA,
D.KLEINER[1] and S.MANIAN
Microbiology Laboratory, Department of Botany
Bharathiar University
Coimbatore – 641 046 Tamil Nadu, India

[1] *Lehrstul für Mikrobiologie*
Universitat Bayreuth
Universitatsstr 30, Postfach 101251
D-95440 Bayreuth, Germany

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ABSTRAK

Kajian telah dibuat terhadap 24 tumbuhan paya bagi menilai peranan ciri-ciri akar ke atas status mikoriza. Jangkitan mikoriza vesikular-arbuskular (VAM) berkait secara positif terhadap ketebalan akar dan secara negatif terhadap bilangan dan panjang rerambut akar. Akar mikoriza kering Bulbostlyis barbata, Cyperus cyperinus, C. kylingia dan Fimbristylis ovata yang berperanan sebagai inokulat kulat VAM dalam kajian kultur pot menunjukkan bahawa akar tumbuhan paya mikoriza boleh bertindak sebagai inokulat dalam merintis dan memulihkan mikoriza dalam tanah semulajadi.

ABSTRACT

Twenty four sedges were examined to assess the role of root characters on mycorrhizal status. Vesicular-arbuscular mycorrhizal (VAM) infection was positively related to root thickness and negatively to root hair number and length. Dried mycorrhizal roots of Bulbostylis barbata, Cyperus cyperinus, C. kyllingia and Fimbristylis ovata served as inocula of VAM fungi in pot culture study indicating that mycorrhizal sedge roots could act as inocula in initiating and reviving mycorrhizae in natural soils.

INTRODUCTION

Root Characters either morphological or physiological affect plant uptake of nutrients from soil. Considerable variations in the root system extensiveness, geometry and plasticity occur between plant species (Brundrett 1991). Root hairs and mycorrhizas represent a way of increasing plant root surface area for modest investment of dry matter. The influence of root morphology on mycorrhizal formation led to the development of "Magnolioid Root Hypothesis" (Baylis 1975). It predicts that plant with coarse roots and with no or few short root hairs develop intense mycorrhizal infection in natural soils compared to those with fine roots and abundant long root hairs. Peat and Fitter (1993) have indicated significant differences in root characters between mycorrhizal and non-mycorrhizal plant species.

The absence or low incidence of mycorrhizae in sedges has been ascribed either to the wet and water logged habitats in which they occur or accumulation of fungal toxic chemicals (Brundrett 1991). Studies conducted by Muthukumar *et al.*(1996) in Western Ghats of Southern India showed the common occurrence of mycorrhizae in several tropical sedges. Another observation made was the rare occurrence of functional mycorrhizae (presence of arbuscules) in sedges as in several non-mycorrhizal plant species. Several members of the Cyperaceae are either non-mycorrhizal or lack functional mycorrhizae (Callaghan *et al.* 1991; Ammani *et al.* 1994). This suggested that mycorrhizae in sedges might be of little importance.

We hypothesised that VAM in poorly mycorrhizal plants could sustain VAM fungal

infectivity in soil during plant inactivity. The objective of the study was two fold. The first objective was to evaluate the role of root characters on mycotrophic status of sedges. The second objective was to determine if mycorrhizal sedge roots could act as source of VAM fungal inoculum.

MATERIALS AND METHODS

Study sites and Their Characteristics

Samples of sedges were collected from five different areas and vegetation types from Western Ghats region in Southern India. Table 1 shows the location site characteristics of the five selected areas.

Sampling

Root and soil samples were collected between March 1993 and June 1995 from five ramdomly selected specimens of the respective sedge species. Sedges were dug out with their entire root system intact, washed thoroughly in water, cut into pieces of 1.0 cm and fixed in FAA (formalin : glacial acetic acid : 70% ethanol, 5:5:90ml). The rhizosphere soil samples collected from sedges were packed in plastic bags and used for soil analyses.

Soil Analysis

The pH of the soil was determined electrochemically in a soil : water suspension (1:1 by weight) using a glass electrode. Chemical analyses were done according to standard procedures (Jackson 1971). The total nitrogen (N) and available phosphorus (P) were determined respectively by micro-Kjeldahl and molybdenum blue methods (Jackson 1971). Exchangeable potassium (K) in the soil was extracted using ammonium acetate solution (pH 7) and measured using a flame photometer (Jackson 1971). Soil organic matter was assessed according to Piper (1950).

Root Morphology

Root diameter was measured in fifty 1-cm-long root pieces and the average of these was recorded for each species. The root pieces were suspended in water on a microscopic slide and the root hair number, length and diameter were measured under a binocular microscope (Itoh and Barber 1983).

Estimation of VAM Fungal Colonisation

Roots were washed free of FAA, cleared in 2.5% KOH (Koske and Gemma 1989), bleached with H_2O_2 and stained with trypan blue (Philips and Hayman 1970). The percentage of root length infected with VAM fungi was estimated accoridng to the magnified intersection method (McGonigle *et al.* 1990).

TABLE 1
Study site characteristics

	Site				
	Coimbatore	Siruvani	Thaisolai	Karumalai	Satyaman-galam
Location	11°04'N & 76° 98' E	10°58'N & 76° 37'E	11°15'N & 76° 35'E	10°32'N & 77°04'E	11°28'N & 76°56'E
Altitude (m MSL)	426-550	500	1850	1200	540
Annual rainfall (mm)	500-700	800-1500	2800-3200	3300-4500	360-600
Vegetation	Scrubs and Grasslands	Forests	Grasslands	Forests	Plantations
Soil characteristics					
Type	Sandy loam	clay loam	Sandy clay loam	clay loam	Red sandy loam
pH	7.62 ± 0.11	7.81 ± 0.21	8.00 ± 0.21	7.5 ± 0.31	7.62 ± 2012
Nutrients (mg kg^{-1})					
Total N	1.15 ± 0.61	1.60 ± 0.40	1.84± 0.74	1.80 ± 0.10	1.42 ± 0.28
Available P	1.10 ± 0.01	1.07 ± 0.05	0.94 ± 0.07	0.90 ± 0.06	1.10 ± 0.24
Exchangeable K	7.81 ± 0.15	2.06 ± 0.40	2.31 ± 0.15	1.64 ± 0.12	4.87 ± 1.12
Organic matter (%)	2.80 ± 0.73	2.66 ± 0.02	4.12 ± 0.68	4.87 ± 1.12	3.96 ± 0.97

Determination of Inoculum Potential

Onion (*Allium cepa* L.), Sunnhemp (*Crotalaria juncea* L) and Cowpea (*Vigna unguiculata* L Walp.) [trap plants] were inoculated with dried roots of *Bulbostylis barbata, Cyperus cyperinus, C. Kyllingia* and *Fimbristylis ovata.* Roots of sedges were obtained from the *Cymbopogon caesius* Stapf., dominated grasslands lying at the base of Maruthamalai hills. The vegetation dies off for a brief period (January to May) prior to the onset of monsoon. Sedge roots were dug out, washed thoroughly free of soil and air dried. After thirty days the roots were sown cut into 2 cm long pieces and 1 g of root was added to each 7.7 cm diameter plastic pots containing 175 g of sterile clay loam soil (pH 5; 1.10 mg Pkg-1). Pots containing sedge roots were sown with seeds of sunnhemp, cowpea and onion bulbs. A 2.5 ml aliquot of the respective crushed nodules was added to each pot containing legumes. No other nutrients were added. The experiment was arranged in a 5 x 3 random factorial design (4 sedge roots plus control and 3 trap plants) with three replications. Trap plants were harvested after 45 days of growth. The inoculum potential of sedge roots was assessed as the quantity of arbuscules, hypae and vesicles developed in the trap plant roots after clearing and staining as described above.

Statistical Analysis

Percentage values of mycorrhizal infection were arcsin transformed (%) and root character values were log transformed prior to statistical analysis. Data on mycorrhizal inoculum potential were subjected to analyses of variance (ANOVA) and the means were separated using Duncan's Multiple Range Test (DMRT). Simple and multiple linear regression analyses were used to assess the relation between root characters and mycorrhizal infection.

RESULTS

The mean root diameter ranged from 0.1 mm in *Eleocharis acutangula* to 0.69 mm in *Carex baccans* (Table 2). Density of root hairs varied from 23 to 221 mm-1 among sedges. The range of root-hair length and diameter of root also differred widely among sedges. Mean percentage of root colonisation was highest in *Scleria lithosperma* (62%) and least in *Cyperus brevifolius* (9%). Sedges with root diameter >0.5 mm, root hair diameter > 0.4 x 10-2 mm and length < 0.5 mm had a higher VAM fungal infection (*Fig.1*). As VAM fungal colonisation was significantly and positively related to root diameter, the mycorrhizal variable was inversely correlated to root hair number and length (*Fig. 2*). However, no correlations were observed between root hair diameter and mycorrhizal infection (r^2 = 0.23, P>0.05). Multiple regression analysis performed with root characters and VAM infection data indicated that root diameter combined with root hair number gave the best combination of predictable values (Table 3). In contrast, root hair length or root diameter gave the least predictable values on mycorrhizal infection. Root hair number was correlated positively to soil P and negatively to soil organic matter (Table 4). A negative correlation also existed between root diameter and soil P.

All the trap plants developed mycorrhizae with typical VAM structures when mycorrhizal sedge roots were used as inoculum (Table 5). However, sunnhemp had non significant variation in total mycorrhizal infection when inoculated with different sedge roots. Cowpea and onion inoculated with roots of *C. cyperinus* and *C kyllingia* developed maximum mycorrhizal infections, but both plant species developed less mycorrhizae when *F. ovata* roots were used as inoculum.

Inoculation with different sedge roots resulted in significant variations in the quantity of VAM structures produced. Inoculation of onion with *Bulbostylis barbata* roots produced maximum arbuscule whereas the same effect was observed in sunnhemp when inoculated with roots of *C. kyllingia* and *F. ovata.* Generally, onion developed less vesicles compared to sunnhemp and cowpea irrespective of the sedge inoculum source. Hyphal formation was higher in roots of onion inoculated with roots of *B. barbata* and *C. cyperinus.* However, sunnhemp and cowpea developed maximum hyphal colonisation when inoculated with roots *F. ovata* and *C. kyllingia* respectively.

DISCUSSION

The present observation indicates that root character is one of the important factors for low incidence of mycorrhizae in sedges. High levels of VAM infection in sedges with root diameter > 0.5 mm and the existence of a positive correlation between the mycorrhizal infection and root diameter confirm the view that mycorrhizae are predominant in coarse rooted species (St. John

TABLE 2
Root characteristics of sedges

Species (Collection site)	Root diameter (mm ± SE)	Root hair density (mm^{-1} ± SE)	Root hair length (mm ± SE)	Root hair diameter (mm ± 10^{-2})	Root colonisation (%)
Bulbostylis barbata (Rottb.) Clarke (A)	0.16 ± 0.02	108 ± 3.69	0.38 ± 0.10	0.55 ± 0.08	47.56 ± 1.14
B. barbata (B)	0.24 ± 0.02	140.00 ± 11.49	0.40 ± 0.13	0.65 ± 0.18	33.47 ± 12.95
B. densa (Wall.) Hand-Mazz. (C)	0.18 ± 0.01	79.00± 8.88	0.34 ± 0.03	0.75 ± 0.09	43.22 ± 4.12
Carex baccans Ness (C)	0.69 ± 0.12	70.00 ± 5.01	0.49 ± 0.05	0.07 ± 0.01	36.99 ± 5.62
C. baccans (D)	0.67 ± 0.16	47.00 ± 4.23	0.26 ± 0.03	0.88 ± 0.01	58.70 ± 6.43
C. lindleyana Nees (C)	0.37 ± 0.05	123.21 ± 5.94	0.25 ' 0.01	0.54 ± 0.01	21.87 ± 25.21
C. myosurus Nees (C)	0.37 ± 0.11	22.73 ± 2.05	0.24 ± 0.01	0.52 ± 0.02	47.71 ± 5.53
C. speciosa Kunth (C)	0.56 ± 0.10	84.00 ± 9.80	0.14 ± 0.01	0.48 ± 0.01	40.00 ± 5.92
Cypreus brevifolius (Rottb.) Hassk (B)	0.18 ± 0.03	124.00 ± 8.53	0.55 ± 0.07	0.51 ± 0.09	9.40 ± 3.92
C. clarkei Cooke (A)	0.43 ± 0.08	79.15 ± 4.69	0.19 ± 0.02	0.45 ± 0.08	26.39 ± 5.92
C. compressus L. (A)	0.18 ± 0.03	80.00 ± 10.61	0.19 ± 0.02	0.34 ± 0.08	24.19 ± 5.95
C. cyperinus (Retz.) Valcken (A)	0.26 ± 0.04	38.46 ± 3.84	0.21 ± 0.01	0.65 ± 0.02	43.38 ± 2.98
C. cyperinus (B)	0.29 ± 0.02	42.31 ± 3.22	0.24 ± 0.01	0.53 ± 0.02	24.46 ± 4.22
C. cyperinus (D)	0.30 ± 0.02	36.81 ± 4.47	0.34 ± 0.01	0.55 ± 0.01	41.67 ± 2.53
C. distans L. f. (B)	0.21 ± 0.02	38.21 ± 4.26	0.67 ± 0.10	0.58 ± 0.01	35.00 ± 9.12
C. dubius (Rottb.) (B)	0.17 ± 0.01	136.00 ± 4.00	0.52 ± 0.07	0.97 ± 0.02	37.13 ± 6.52
C. iria L. (A)	0.46 ± 0.05	168.33 ± 3.53	0.72 ± 0.12	0.92 ± 0.40	32.00 ± 4.38
C. iria (A)	0.39 ± 0.05	153.42 ± 4.39	0.70 ± 0.03	0.90 ± 0.01	13.67 ± 6.28
C. kyllingia Endlicher (B)	0.28 ± 0.03	121.26 ± 0.70	0.55 ± 0.08	0.41 ± 0.01	11.13 ± 2.70
C. nutans Vahl (B)	0.67 ± 0.02	40.36 ± 5.44	0.50 ± 0.44	0.53 ± 0.01	48.21 ± 9.56
C. paniceus (Rottb.) Brockeler (B)	0.24 ± 0.04	102.00 ± 6.80	0.28 ± 0.01	0.78 ± 0.01	21.33 ± 13.12
C. rotundus L. (A)	0.15 ± 0.02	120.00 ± 4.94	0.29 ± 0.01	0.43 ± 0.10	20.52 ± 3.42
C. rotundus (B)	0.14 ± 0.01	123.21 ± 4.06	0.28 ± 0.01	0.48 ± 0.09	19.73 ± 8.18
C. rotundus (E)	0.15 ± 0.01	128.36 ± 6.29	0.25 ± 0.02	0.43 ± 0.14	13.31 ± 4.36
C. squarrosus L. (B)	0.25 ± 0.02	93.00 ± 5.97	0.46 ± 0.07	0.58 ± 0.15	44.88 ± 12.81
C. triceps (Rottb.) Endlicher (B)	0.20 ± 0.02	138.00 ± 4.90	0.67 ± 0.18	0.64 ± 0.17	16.38 ± 8.10
Eleocharis acutangula (Roxb.) Schultes (B)	0.10 ± 0.01	64.00 ± 3.40	0.38 ± 0.01	0.63 ± 0.14	19.46 ± 10.15
Fibristylis consanguinea Kunth (B)	0.43 ± 0.04	80.36 ± 1.84	0.17 ± 0.01	0.43 ± 0.08	58.33 ± 10.15
F. falcata (Vahl.) Kunth (A)	0.45 ±0.02	222.00 ± 15.55	0.58 ± 0.09	0.62 ± 0.11	28.20 ± 3.63
F. ovata (Burm. F.) Kern (A)	0.25 ± 0.06	75.00 ± 2.24	0.33 ± 0.01	0.54 ± 0.10	25.86 ± 10.26
Scleria lithosperma L. SW. (A)	0.46 ± 0.16	108.00 ± 3.96	0.18 ± 0.01	0.60 ± 0.09	32.00 ± 7.14
S. lithosperma (B)	0.43 ± 0.07	96.00 ± 7.48	0.14 ± 0.01	0.58 ± 0.17	61.67 ± 21.15

A, B, C, D and E – Coimbatore, Siruvani, Thaisolai, Karumalai and Satyamangalam respectively

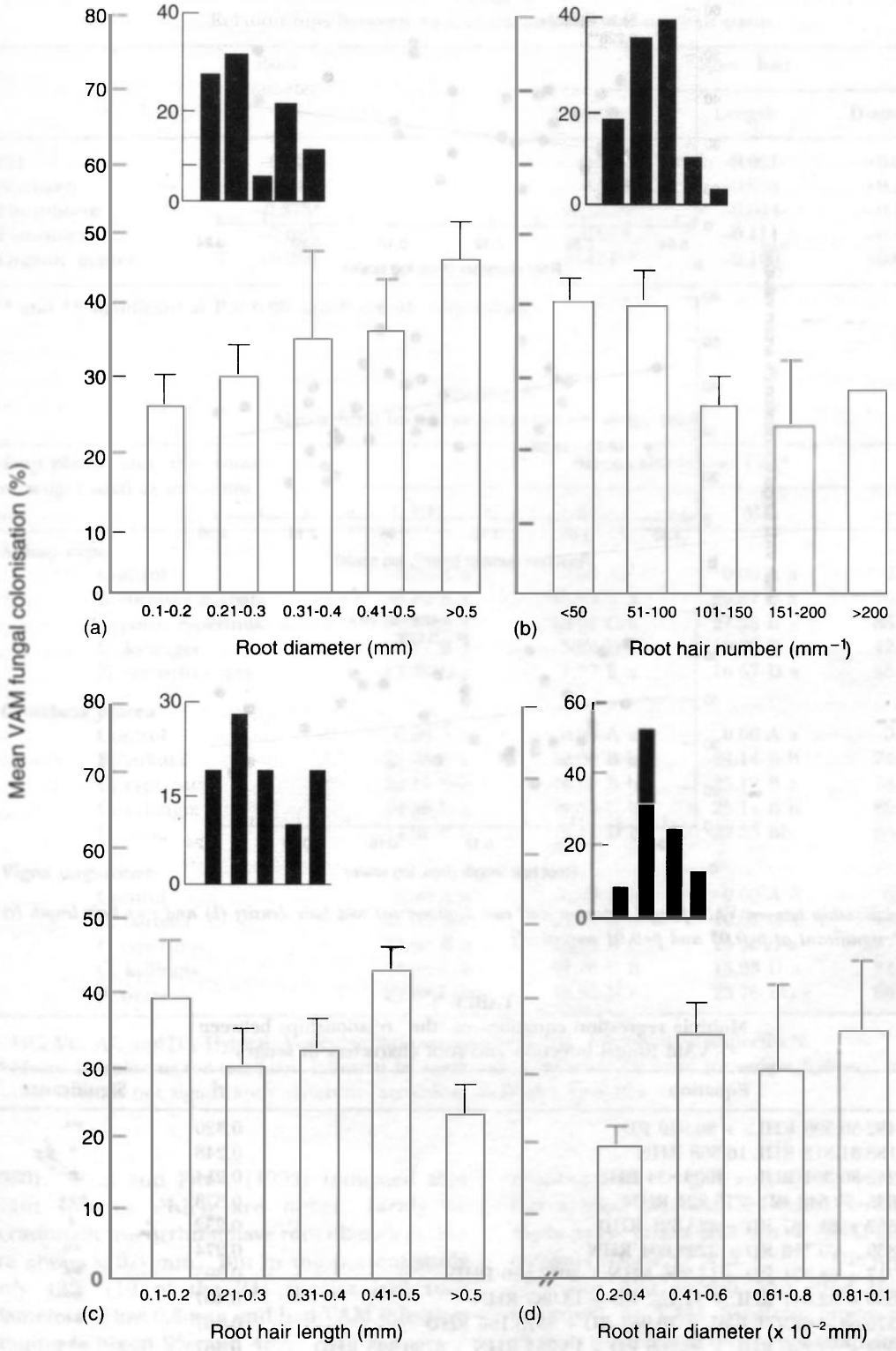

Fig 1. Mean VAM colonisation of different root diameter (a), root hair number (b), length (c) diameter (d) classes (vertical bars indicate ±1 S.E). Inserted histograms present the frequency of species in a class range

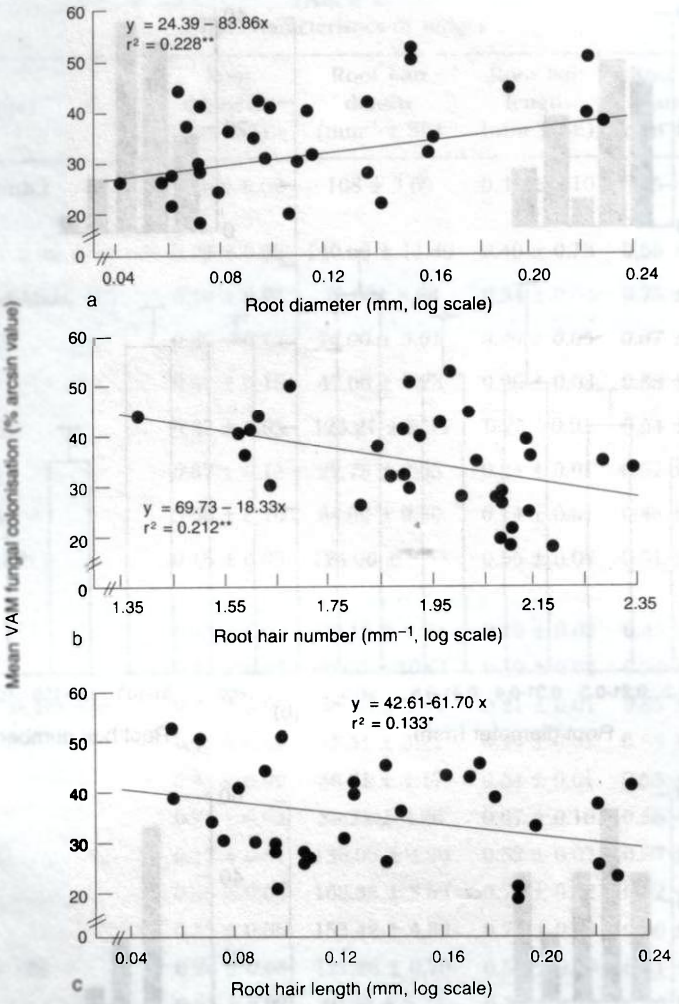

*Fig 2. Relationship between VAM fungal infection and root diameter (a) root hair density (b) and root hair length (c). * ** significant at p<0.05 and p<0.01 respectively*

TABLE 3
Multiple regression equations of the relationships between VAM fungal infection and root characters in sedges

Equation	r^2	Significance
Y = 31.482-50.395 RHLa + 80.949 RD	0.320	**
Y = 70.188-31.812 RHL-16.368 RHN	0.248	*
Y = 32.242-80.351 RHL + 4903.834 RHD	0.214	*
Y = 56.635+70.648 RD – 15.824 RHN	0.373	***
Y = 22.552 + 81.467 RD + 823.621 RHD	0.232	*
Y = 65.839 – 20.713 RD + 3292.694 RHN	0.274	**
Y = 54.717 + 63.971 RD – 17.206 RHN + 2077.556 RHD	0.395	**
Y = 55.659 – 32.847 RHL + 71.132 RD – 13.085 RHN	0.407	**
Y = 26.370.68 – 68.771 RHL + 70.957 RD + 3375.180 RHD	0.367	**
Y = 51.592 – 52.226 RHL + 59.266 RD – 13.983 RHN + 3780.393 RHD	0.467	***

*, ** and *** Significant at P < 0.05, P < 0.01 and P < 0.001 respectively.

[a]RHL – Root hair length; RD – root diameter; RHN – Root hair number and RHD – Root hair diameter.

TABLE 4
Relationships between root characters and soil nutrient status

	Root Diameter	Root hair		
		Number	Length	Diameter
PH	–0.121	–0.031	–0.061	+0.058
Nitrogen	+0.144	–0.309	+0.088	+0.160
Phosphorus	–0.375*	+0.483**	–0.044	–0.159
Potassium	–0.021	+0.063	–0.111	–0.112
Organic matter	+0.256	-0.474**	–0.100	+0.057

* and ** significant at $P < 0.05$ and $P < 0.01$, respectively

TABLE 5
Mycorrhizal inoculum potential of sedge roots

Trap plants and the roots of sedges used as inoculum	Root colonisation (%)*			
	HC	VC	AC	TC
Allium cepa				
Control	0.00 A a**	0.00 Aa	0.00 A a	0.00 A a
Bulbostylis barbata	36.19 B a	10.55 B a	29.87 B a	76.60 B b
Cyperus cyperinus	37.39 C a	19.02 C a	27.58 B a	85.99 C b
C. kyllingia	27.27 B a	5.32 D a	10.09 C a	42.68 D c
Fimbristylis ovata	17.05 D a	1.97 E a	16.57 D a	35.58 E d
Crotalaria juncea				
Control	0.00 A a	0.00 A a	0.00 A a	0.00 A a
B barbata	28.43 b a	22.00 B b	24.14 B b	74.56 B a
C. cyperinus	28.14 B b	24.00 B b	25.19 B a	78.60 B a
C. kyllingia	24.56 B a	39.59 C b	25.14 B b	89.29 B b
F. ovata	44.61 C a	6.11 D b	32.53 Bb	83.11 B b
Vigna unguiculata				
Control	0.00 A a	0.00 A a	0.00 A A	0.00 A a
B. barbata	27.62 B b	25.74 B b	20.65 C a	74.10 B a
C cyperinus	28.83 B b	23.10 B c	25.36 B a	77.33 B a
C. kyllingia	38.99 C b	32.26 C b	13.63 D a	84.85 C b
F. ovata	22.88 C b	19.52 D c	23.76 BC c	66.16 D c

* HC, VC, AC andTC, Hyhhal, Vesicular, Arbuscular and Total colonisation respectively.
** Means in columns for test plant followed by same high case letter (s) and for sedges followed by same low case letter is not significantly different according to DMRT ($p<0.05$).

1980). Peat and Fitter (1993) indicated that plant species which are never, rarely or occasionally mycorrhizal have root diameters that are always < 0.3 mm. But in the present study only 42% (10 of the 24) species had root diameters below 0.3 mm and had VAM infection ranging between 9% and 48%.

Sedges with long and numerous root hairs had less VAM infection compared to sedges with less and short root hairs. Further, root hair number and length negatively correlated to mycorrhizal infection. Similiar observations were made in rye plants (Baon *et al.* 1994) and banana cultivars (Declerck *et al.* 1995). The low r^2 value of root hair length and total root length colonised by VAM fungi in linear regression analysis suggest that other root characters besides root hair length affect VAM colonisation. This statement is further supported by a higher r^2 value in the interaction between root diameter

and root hair number on VAM fungal infection in multiple regression analysis compared to the interaction values of root hair length with other root characters.

The existence of a positive correlation between soil P and root hair density supports the observation of Hetrick (1991) who reported the unstable nature of root hair density to the changing soil P. Although this result contrasts earlier reports where an inverse relation between root hair density and substrate P has been reported (Bhat and Nye 1974; Brewster *et al.* 1976) but supports other reports where a positive relation has been reported (Baylis 1970; Barley and Roviara 1970).

The inverse correlation between root diameter and soil P contrasts the observation of Powell (1974) who found that the non-mycorrhizal *Carex coriacea* plants developed finer roots when grown in P deficient soil and thicker roots in P fertile soils. Several graminiods including sedges allocate more carbon to roots (Callaghan *et al.* 1991) and the highly developed root hairs increase the root surface area making mycorrhizae less critical. In a recent study (Muthukumar *et al.* 1996) a three fold increase in VAM infection in purple nutsedge *(C. rotundus)* was associated with a two fold decrease in tissue P concentration. However, in natural conditions sedges can take up and accumulate P even in deficient soils.

The initiation of mycorrhizae in trap plants by mycorrhizal sedge roots supports previous findings that mycorrhizal roots are an important source of inoculum in natural soils (Abbott and Robson 1991). Many VAM fungal species are known to regrow from root fragments that are either fresh or dry and can remain infective upto six months within roots (Tommerup and Abbott 1981). While such a survivability was not tested in this study, the results obtained raise the possibility that mycorrhizal sedge roots could remain infective during the dry season also.

As most sedges are perennials, the inoculum surviving in their root may revive infection during the onset of the wet season like the site from where roots were collected to test infectivity. Additionally dead roots of sedges remain intact for long periods (Muthukumar personal obersvation). Roots that are protected from decomposition by various soil physical and biological factors provide the intraradical propagule an advantage over soil borne propagules. Further, perennials have an advantage of intraradical propagules because new roots often grow in channels of old roots. The placement of new roots adjacent to root-borne propagules, rapidly initiate mycorrhizal formation.

Though studies by Tommerup and Abbott (1981) suggested that the time required for root inoculum to initiate mycorrhizae is four weeks. However the present study indicates that it may be quite rapid, since at the first six weeks > 70% of the rap root plants became mycorrhizal. However, the total mycorrhizal infection and root length colonised by VAM structures varied greatly among trap plants. This is in accordance with the view that the dependence of host plant influences mycorrhizal infection (Simpson and Daff 1990). Onion, a highly mycorrhizal dependent host compared to cowpea developed less infection when inoculated with sedge root inoculum of *C. kyllingia* and *F. ovata* suggesting that mycorrhization in some hosts depends on the inocula type (Jarstfer and Sylvia 1993).

The present study clearly indicates the role of root characters on the mycorrhizal status of sedges. Further, inocula surviving in the roots of sedges serve as an important source of inoculum for new roots arising the next season, thus increasing and sustaining mycorrhizal infectivity in natural soils. This may enable the later establishment of mycorrhizal dependent species in sites having low VAM fungal propagule.

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